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Molecular phylogeny of Chromadorea supports genus reclassification of Desmodorida and Microlaimida with the description of two new species from the Yellow Sea, China

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Abstract

Phylogenetic relationships within the marine Chromadorea are complex, and the taxonomic positions at the family and genus levels remain flexible due to discrepancies between morphological and molecular evidence. During our taxonomic study in the Yellow Sea, two species, *Pseudochromadora crispata* **sp. nov.** and *Microlaimus parakoranus* **sp. nov.**, are described. *Pseudochromadora crispata* **sp. nov.** is characterized by a short body, a coarsely annulated cuticle with lateral alae, a unispiral amphidial fovea, slightly curved spicules, a gubernaculum plate shaped with a cuticularized lateral piece, four ventral precloacal copulatory thorns, and one pair of postcloacal thorns. *Microlaimus parakoranus* **sp. nov.** is characterized by a finely striated cuticle, short cephalic setae, a cryptocircular amphidial fovea, the absence of somatic setae, slightly curved spicules with swollen proximal ends, a heavily cuticularized gubernaculum, and a conical tail with a slightly cylindrical distal end. Phylogenetic analysis within Chromadorea indicates that the genera *Promodesmodora* and *Molgolaimus* should be transferred to Chromadorida, the genera *Nudora* and *Monoposthia* should be removed from Microlaimida based on morphological and molecular evidence, and *Onepunema* should be kept in Desmodoridae despite its anomalous phylogenetic position.

Key Words

Chromadorea, free-living nematode, phylogenetic analysis, taxonomy

Introduction

Nematodes are the most abundant metazoan taxon in aquatic sediments and one of the most diverse groups, with only 10–15% of species identified (Hodda 2022; Leduc and Zhao 2023). Convergent evolution, scarcity of diagnostic characters, and the limited availability of DNA barcoding sequences have rendered nematodes one of the most challenging and complex taxonomic groups (Leduc et al. 2017). Recently, genomic DNA and transcriptome RNA have been used to elucidate nematode origins and relationships (Lee et al. 2023; Xue et al. 2025); however, the limited availability of genomic DNA and transcriptome RNA sequences has hindered progress in nematode phylogenetic reconstruction. The increasing number of rDNA sequences, particularly small subunit (SSU) and large subunit (LSU) D2–D3 sequences, has significantly advanced our understanding of nematode evolution despite the existence of paraphyletic and polyphyletic groups (Ahmed and Holovachov 2021; De Ley and Blaxter 2004).

The family Desmodoridae is a diverse and heterogeneous group mostly occurring in marine habitats. Desmodoridae is described as a highly polyphyletic group lacking a synapomorphy in the superfamily Desmodoroidea (van Megen et al. 2009). According to Tchesunov (2014), three families – Desmodoridae, Epsilonematidae, and Draconematidae – form the Desmodoroidea, with the synapomorphy of only the anterior testis being present (Lorenzen 1981, 1994). However, the genus *Onepunema*,

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with two outstretched testes, altered the status of Desmodoroidea from monophyletic to paraphyletic, which caused uncertainty in the taxonomic position of *Onepunema* (Armenteros et al. 2014a; Leduc and Verschelde 2015). The family Microlaimidae was initially placed in Chromadorida by Jensen (1978) and subsequently transferred to Desmodorida by Lorenzen (1981, 1994) based on the outstretched ovaries, and later to Microlaimida by Leduc et al. (2017) based on molecular sequences. The taxonomic position of *Molgolaimus* – once classified in Microlaimidae – was contentious, with morphological evidence suggesting classification in Desmodorida and molecular evidence supporting placement in Chromadorida (Leduc et al. 2019; Manoel et al. 2025). The taxonomic position of *Prodesmodora* – once classified in Microlaimidae by Jensen (1978) – was also flexible for these specialized freshwater and terrestrial inhabitants with parthenogenetic reproduction. Morphological and molecular evidence show it to be closely related to Chromadorida and Microlaimida (van Megen et al. 2009; Leduc et al. 2017; Guo et al. 2023; Manoel et al. 2025). With more SSU and LSU sequences deposited in GenBank, the phylogenetic tree within the basal chromadorean orders Chromadorida, Desmodorida, and Microlaimida is expected to elucidate their taxonomic positions.

To study the diversity and taxonomy of free-living marine nematodes in the intertidal zone of the Yellow Sea in China, undisturbed sediments have been collected since July 2023. Marine nematodes are the dominant meiofauna group, and more than 200 nematode species have been discovered (Guo et al. 2023; Liang et al. 2024). In this article, two new species, *Pseudochromadora crispata* sp. nov. and *Microlaimus parakoreanus* sp. nov., are described. Ribosomal DNA sequences (LSU and SSU) from both species were also obtained, and phylogenetic analyses within the families Microlaimidae and Desmodoridae are presented.

Materials and methods

Specimen collection and preparation

Undisturbed sediment samples were collected with a syringe (2.9 cm inner diameter) from the sublittoral region of Yancheng Beach, Jiangsu Province, China, since July 2023. Sediment samples used for morphological analysis were fixed with 10% formalin, and those used for molecular analysis were fixed with 95% ethanol. In the laboratory, formalin-fixed sediment samples were stained with Rose Bengal overnight and rinsed through two sieves with mesh sizes of 500 µm and 45 µm to isolate meiofauna from macrofauna (>500 µm). Heavier sediment particles were removed by centrifugation in Ludox-TM (Sigma-Aldrich Co., USA) three times. Meiofauna were transferred to a grid-lined Petri dish and sorted under a stereoscopic microscope. Nematodes were transferred into a mixture of ethanol (5%) and glycerin (5%), with the ethanol slowly evaporated, and subsequently mounted in glycerin on permanent slides. Observations and measurements were made using an AxioScope-5 differential interference contrast microscope (Zeiss, Germany). Line drawings were created with ZEN 3.7 Labscope software using an iPad (Apple, USA). The type specimens were deposited at the College of Agriculture and Biology, Liaocheng University, China.

Samples used for molecular analysis were treated in the same way as the formalin-fixed samples, but without staining. One male specimen of *Pseudochromadora crispata* sp. nov. and one male specimen of *Microlaimus parakoreanus* sp. nov. were sorted. Identification was confirmed primarily based on buccal cavity shape, cephalic setae, spicule and gubernaculum shape, and tail morphology on temporary slides.

DNA extraction, PCR amplification, and phylogenetic inference

Genomic DNA was extracted with the DNeasy Blood & Tissue Kit (Qiagen, Germany) and used as the template for SSU and LSU amplification. Primers G18S4F (5'-GCT TGT CTC AAA GAT TAA GCC-3') and 18PR (5'-TGA TCC WMC RGC AGG TTC AC-3') were used for nearly full-length SSU (Blaxter et al. 1998), and primers D2A (5'-ACA AGT ACC GTG AGG GAA AGT TG-3') and D3B (5'-TCG GAA GGA ACC AGC TAC TA-3') were used for the D2–D3 fragment of LSU (Nunn 1992). PCR was conducted as described by Zhao et al. (2015). LSU and SSU were sequenced by Genewiz (China). The newly obtained SSU sequences (accession numbers: *Pseudochromadora crispata* sp. nov., PV981972; *Microlaimus parakoreanus* sp. nov., PV981960) and D2–D3 LSU sequences (*Pseudochromadora crispata* sp. nov., PV983853; *Microlaimus parakoreanus* sp. nov., PV983853) have been deposited in GenBank.

SSU sequences longer than 600 bp and D2–D3 fragments of LSU from the orders Desmodorida, Chromadorida, and Microlaimida were retrieved from GenBank. To facilitate the analysis, one sequence from each genus was selected. Forty-three SSU and LSU sequences derived from the same specimens, along with 47 additional SSU sequences, were used for phylogenetic analysis (Table 1) and rooted with *Viscosia dossena* Leduc & Zhao, 2023 (accession numbers OK317193, OK317218), *Enoplolaimus lenunculus* Wieser, 1959 (accession numbers PQ404814, PQ404816), and *Enoploides parakoreanus* Meng, Liang, & Wang, 2025 (accession numbers PQ404817, PQ404815). A dataset of concatenated LSU + SSU sequences was constructed with PhyloSuite v. 1.2.3. Alignment was performed using the MAFFT v. 7 algorithm. Substitution models (GTR [general time-reversible] + G [gamma distribution] + I [proportion of invariable sites]) were selected for Bayesian inference (BI) analyses. Maximum likelihood (ML) analysis was performed using PhyloSuite v. 1.2.3 with 1,000 bootstrap replicates. Bayesian inference was conducted using

Table 1. Sequence information of SSU and LSU used in the phylogenetic analysis of the orders Desmodorida, Chromadorida, and Microlaimida.

Species	SSU accession number	LSU accession number	Specimen voucher
Acanthonchus tridentatus	OQ396722	OQ417523	10a, 10c
Acanthopharynx micans	OP137155	OP137147	TAV25
Achromadora sp.	AY284718	–	–
Actinonema pachydermatum	OR590910	–	S213_13
Aponema pseudotorosum	MK446237	MK446242	TAN1708-NNCNZ3324
Atrochromadora microlaima	AY854204	–	–
Bendiella longicauda	KU746879	KU746884	–
Bolbolaimus major	OQ835637	OQ835636	7-21
Bradylaimus suecicus	MW078526	OR589659	S228_8
Calomicrolaimus sp1	MG669708	–	Ugent_CeMoFe71P14E14_18S
Catanema schiemeri	MW267953	–	V015
Cheironchus sp.	LK054721	–	–
Chromadoropsis vivipara	OR590945	–	S226_19
Chromadora cf. *nudicapitata*	OK317199	OK317224	NNCNZ3377
Chromadorella filiformis	OR590912	–	S209_1
Chromadorina communis	PQ396187	PQ412514	4-2
Chromadorita leuckarti	FJ969119	–	–
Chromaspirina pellita	OR590950	OR589677	S178_35
Choniolaimus papillatus	MN786721	MN786742	S228_12
Cobbionema acuminata	OR590996	–	S178_60
Cyatholaimus sp.	OQ065240	OQ054307	A63
Desmodora communis	OR590947	–	sensu Platt & Warwick S207_10
Desmodorella verscheldei	KR080526	KR265063	–
Demonema rapax	MN786724	MN786748	HYNC4677-2
Denticulella sp.	OR590916	–	S210_2
Dichromadora media	OR479913	OR479918	3-33
Dracognomus tinae	MG669760	–	Ugent_CeMoFe25X6L14_18S
Dracograllus ngakei	KR080527	KR265064	–
Draconema cephalatum	OR590960	OR589693	S240_1
Endeolophos sp.	MG669765	–	Ugent_CeMoFe57X18B15_18S
Enoploides parakoreanus	PQ404817	PQ404815	3-4
Enoplolaimus lenunculus	PQ404814	PQ404816	3-2
Epsilonema dentatum	KR080528	KR265065	–
Ethmolaimus pratensis	AY593942	–	–
Eubostrichus dianeae	LR746218	–	–
Euchromadora ezoensis	OQ396717	OQ417519	2a_2c
Gammanema rapax	MN786725	MN786749	S226_12
Gomphionema parvum	MG669781	–	Ugent_CeMoFe89H6K12_18S
Graphonema sp.	MH302889	–	USNM:IZ:1502138
Halichoanolaimus funestus	PQ286530	PQ301197	TAN2402-3
Hypodontolaimus minus	PQ249718	PQ283889	2-3
Innocuonema tentabunda	OR590929	–	S227_12
Ixonema powelli	OL388482	OR589722	S178_55
Latronema dyngi	MN786739	MN786764	S208_7
Laxus sakihariiae	MF997604	MF997600	–
Leptonemella aphanothecae	LR746210	–	–
Longicyatholaimus subtenuis	MG669844	–	Ugent_CeMoFe26H6K12_18S
Marylynnia sp.	PV244260	–	–
Microlaimus parakoreanus sp. nov.	PV981960	PV983853	–
Molgolaimus kaikouraensis	MK446235	MK446240	TAN1708-NNCNZ3322
Molgolaimus demani	AY854220	–	–
Monoposthia mirabilis	MW078504	OR589735	S226_16
Metachromadoroides remanei	MG669855	–	Ugent_CeMoFe3C16A12_18S
Metacyatholaimus delicatus	KX270433	KX270434	–
Nannolaimoides sp.	PP859969	–	NBC1.28_Nannolaimoides
Neochromadora parabilineata	OR126985	OR135360	11-18
Nudora ilhabelae	JQ071928	–	–
Onepunema enigmaticum	MK446238	MK446243	TAN0705-157

Species	SSU accession number	LSU accession number	Specimen voucher
Onyx cangionensis	MG669913	–	Ugent_CeMoFe129H6K12_18S
Paracanthonchus miltommatus	KX270431	KX270432	–
Paracyatholaimus vitraeus	OR161038	–	ZUEC-PIC 788
Paracyatholaimoides sp.	OR714868	–	S178_24
Paradesmodora immersa	LK054702	–	–
Paradraconema jejuense	FJ182220	–	–
Paraethmolaimus appendixocaudatus	OQ001134	–	Q52
Paralongicyatholaimus sp.	OQ076327	–	F47
Parapinnanema sp.	PP859948	–	KBS2.15_Parapinnanema
Perepsilonema corsicum	OL388476	OR589698	S178_46
Pomponema sp.	OP548510	OR148452	ZUEC-PIC 700
Praeacanthonchus punctatus	OR714873	–	S228_27
Prochaetosoma sp.	KX944156	–	–
Prochromadora sp.	EF591341	–	–
Prochromadorella obtusidens	OR590937	–	S207_3
Prodesmodora circulata	AY284720	–	–
Pseudocheironchus ingluviosus	KU746882	KU746887	–
Pseudochromadora crispata sp. nov.	PV981972	PV997437	–
Pseudomicrolaimus dentatus	OR590990	–	GT10_16
Pseudonchus virginiae	MK446239	MK446244	TAN0705-45
Ptycholaimellus ocellatus	OQ538290	OQ466609	12a, 12c
Punctodora ratzeburgensis	KJ636232	–	–
Rhips paraornata	MG669994	–	Ugent_CeMoFe2C19F12_18S
Richtersia bispinata	MN163132	–	–
Robbea hypermnestra	KJ414466	–	–
Spiliphera cf. *dolichura/gracilicauda*	MK626778	–	18P6G16_Spiliphera_dolichura_or_gracilicauda
Spilophorella sp.	OQ065318	OQ054306	F78
Spirinia parasitifera	MW078522	OR589684	S226_9
Stilbonema majum	LR746215	–	–
Synonchiella rotundicauda	KU746883	KU746888	–
Synonchium iranicum	MN158139	–	–
Viscosia dossena	OK317193	OK317218	NNCNZ3371
Xyzzors sp.	Y16923	–	–
Zalonema sp.	MT604123	MT649462	Zalonema_929

CIPRES and MrBayes v. 3.2.7a with a chain length of 10,000,000 and a burn-in fraction of 0.25. The topologies of the resulting trees were visualized using FigTree v. 1.4.3 and refined with PowerPoint 2021.

SSU sequences longer than 600 bp and D2–D3 fragments of LSU from Desmodoridae and Microlaimidae were retrieved from GenBank. In total, 25 SSU and LSU sequences derived from the same specimen, along with 43 additional SSU sequences, were used for phylogenetic analysis (Table 2). A dataset of concatenated LSU + SSU sequences was constructed with PhyloSuite v. 1.2.3. Alignment was performed using the MAFFT v. 7 algorithm. Substitution models (GTR [general time-reversible] + G [gamma distribution] + I [proportion of invariable sites]) were selected for Bayesian inference (BI). The analysis was rooted with *Enoplolaimus lenunculus* Wieser, 1959 (accession numbers PQ404814, PQ404816). ML and BI tree construction and refinement were conducted as in the previous analysis.

Abbreviations are as follows: a, body length/maximum body diameter; a.b.d., anal body diameter; b, body length/pharynx length; c, body length/tail length; c.b.d., corresponding body diameter; c′, tail length/a.b.d.; V%, position of vulva from the anterior end expressed as a percentage of total body length.

Results and discussion

Morphological characterization

Systematic of *Pseudochromadora crispata* sp. nov.

Family Desmodoridae Filipjev, 1922

Genus *Pseudochromadora* Daday, 1899

***Pseudochromadora crispata* sp. nov.**

https://zoobank.org/734C1C10-6B88-4A01-B3BB-05792A845017

Figs 1–3, Table 3

Type material. Four males and three females were collected from Station RCHW in May 2024. Holotype: m#1 on slide number 24RCHW 8-1-54, paratypes: m#2 24RCHW 8-1-204, m#3 24RCHW 8-1-52, m#4 24RCHW 8-1-38 and f#1 on 24RCHW 8-2-72, f#2 on 24RCHW 8-1-200, f#3 on 24RCHW 8-1-12.

Table 2. Sequence information of SSU and LSU used in the phylogenetic analysis of the families Desmodoridae and Microlaimidae.

Species	SSU accession number	LSU accession number	Specimen voucher
Acanthopharynx dormitata	KX077908	KX077909	–
Acanthopharynx micans	OP137155	OP137147	TAV25
Acanthopharynx parva	OP137152	OP137150	TAV15
Aponema pseudotorosum	MK446237	MK446242	TAN1708-NNCNZ3324
Bolbolaimus major	OQ835637	OQ835636	7-21
Bolbolaimus distalamphidus	PQ435316	PQ358938	1-8
Bradylaimus suecicus	MW078526	OR589659	S228_8
Calomicrolaimus sp.	MG669708	–	Ugent_CeMoFe71P14E14_18S
Calomicrolaimus parahonestus	AY854218	–	–
Catanema schiemeri	MW267953	–	V015
Catanema exile	LK054707	–	–
Chromadoropsis vivipara	OR590945	–	S226_19
Chromaspirina pellita	OR590950	OR589677	S178_35
Chromaspirina stilbonematinops	OK317205	–	NNCNZ3383
Chromaspirina parapontica	MT846146	–	S219-2
Desmodora bilacinia	KX077910	KX077911	–
Desmodora pontica	OR590949	–	S153_6
Desmodora communis	OR590947	–	sensu Platt & Warwick S207_10
Desmodora scaldensis	OQ538291	–	–
Desmodora marci	JX463180	–	–
Desmodora ovigera	Y16913	–	–
Desmodorella tenuispiculum	MW078515	OR589674	S232_2
Desmodorella schulzi	MT846159	–	S178-25
Desmodorella verscheldei	KR080526	KR265063	–
Eubostrichus dianeae	LR746218	–	–
Eubostrichus cf. *topiarius*	LR746196	–	–
Enoplolaimus lenunculus	PQ404814	PQ404816	3-2
Eubostrichus parasitiferus	Y16916	–	–
Ixonema powelli	OL388482	OR589722	S178_55
Laxus cf. *cosmopolitus*	LR746202	–	
Laxus oneistus	LR746201	–	
Laxus oneistus	KT826596	–	–
Laxus parvum	LK054709	–	
Laxus sakihariiae	MF997604	MF997600	–
Leptonemella aphanothecae	LR746210	–	–
Leptonemella brevipharynx	LK054704	–	–
Leptonemella vicina	KU921474	–	–
Leptonemella cf. *vestari*	KP943963	–	–
Leptonemella cf. *juliae*	KP943962	–	–
Metachromadora cf. *vulgaris minor*	MK626772	–	9P6G16_Metachromadora_vulgaris_or_minor
Metachromadora gerlachi	LK054712	–	–
Metachromadora orientalis	MG669854	–	Ugent_CeMoFe91H6K12_18S
Metachromadoroides obscura	MK626816	–	87P19G16_Metachromadoroides_obscura
Metachromadoroides remanei	MG669855	–	Ugent_CeMoFe3C16A12_18S
Microlaimus compridus Ugent	MG669879	–	Ugent_CeMoFe1X6K14_18S
Microlaimus cyatholaimoides	MG669882	–	Ugent_CeMoFe21C18A_18S
Microlaimus honestus	MG669885	–	Ugent_CeMoFe4X6K14_18S
Microlaimus korari	OK317206	OK317228	NNCNZ3384
Microlaimus orientalis	MG669886	–	Ugent_CeMoFe95P29E14_18S
Microlaimus papillatus	PQ432931	PQ433003	LJW-21-13
Microlaimus parakoreanus sp. nov.	PV981960	PV983853	3-1
Microlaimus robustidens	OL388481	OR589726	S178_45
Onepunema enigmaticum	MK446238	MK446243	TAN0705-157
Onyx cangionensis	MG669913	–	Ugent_CeMoFe129H6K12_18S
Paradesmodora immersa	LK054702	–	–
Pseudochromadora thinaica	MZ958846	MZ958839	–
Pseudochromadora plurichela	OK317204	–	NNCNZ3382

Species	SSU accession number	LSU accession number	Specimen voucher
Pseudochromadora crispata sp. nov.	PV981972	PV997437	9-1
Pseudomicrolaimus dentatus	OR590990	–	GT10_16
Pseudonchus virginiae	MK446239	MK446244	TAN0705-45
Robbea hypermnestra	KJ414466	–	–
Robbea agricola	KJ414464	–	–
Robbea ruetzleri	KJ414465	–	–
Robbea porosum	LK054714	–	–
Spirinia antipodea	MH472584	MH472585	NNCNZ3315
Spirinia parasitifera	MW078522	OR589684	S226_9
Stilbonema brevicolle	LK054711	–	–
Stilbonema majum	LR746215	–	–
Zalonema sp.	MT604123	MT649462	Zalonema_929

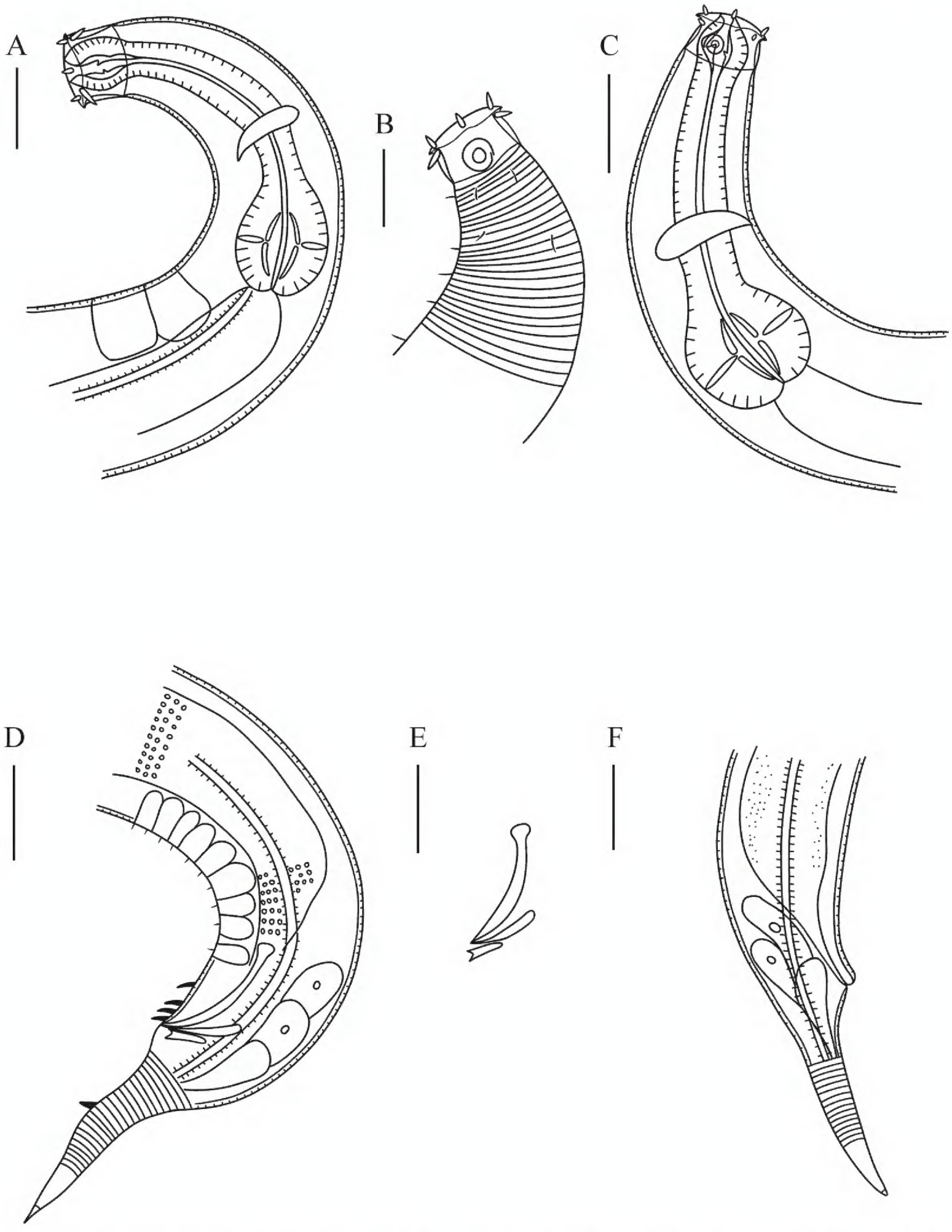

Figure 1. *Pseudochromadora crispata* sp. nov. **A.** Lateral view of the male anterior region, showing the pharynx region; **B.** Lateral view of the male anterior region; **C.** Lateral view of the female anterior region; **D.** Lateral view of the male posterior region; E spicules and gubernaculum; **F.** Lateral view of the female posterior region. Scale bars: 20 µm (**A, B**); 30 µm (**C–F**).

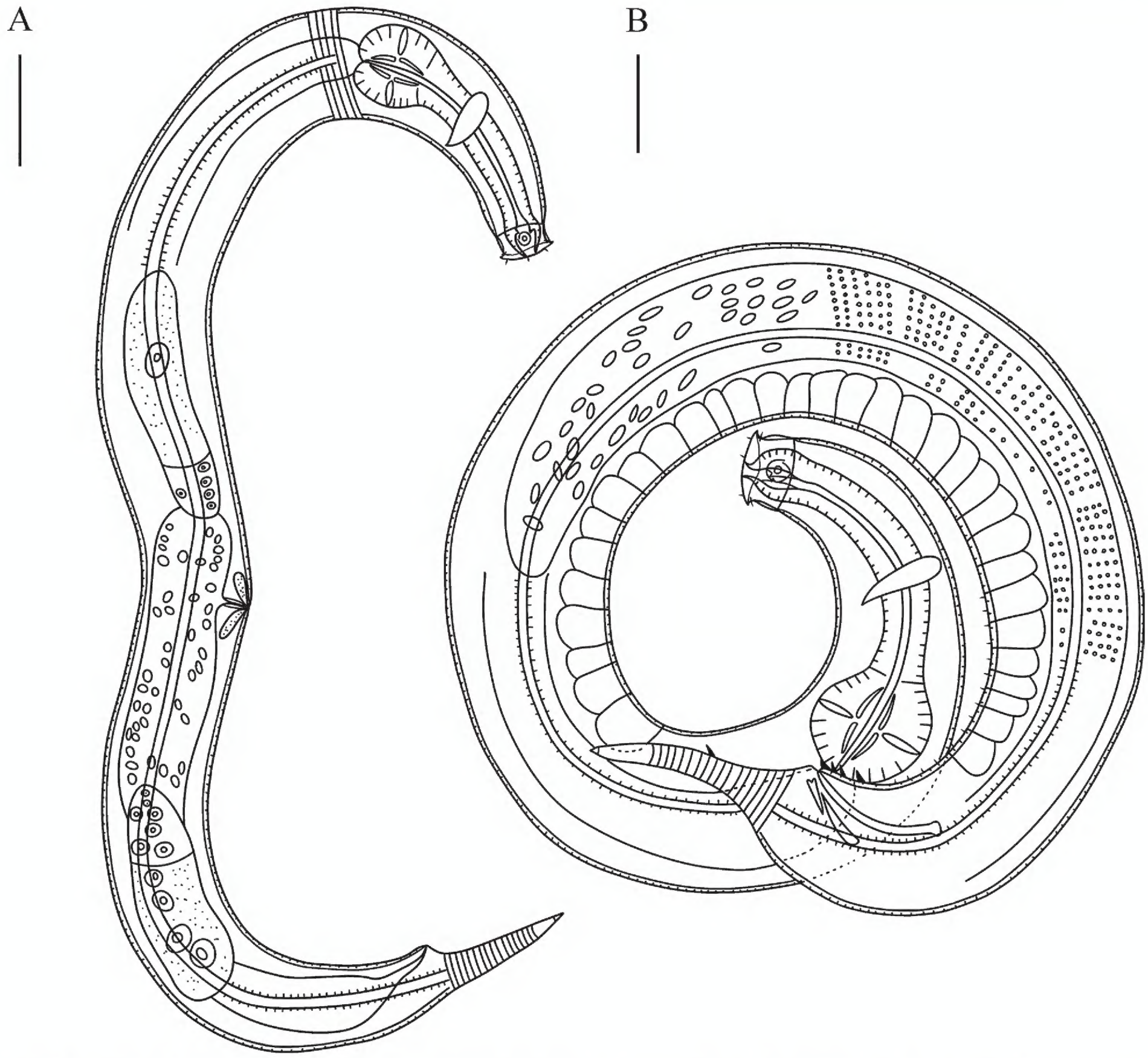

Figure 2. *Pseudochromadora crispata* sp. nov. **A.** Lateral view of the female entire body; **B.** Lateral view of the male entire body. Scale bars: 50 μm (**A, B**).

Type locality and habitat. All specimens were collected from the Yancheng coast, Jiangsu Province, China. 33°2'N, 120°51'E (RCHW), 0–8 cm sediment depth, sandy sediment.

Etymology. The specific name refers to the nematode always being curled when fixed with formalin.

Measurement. All measurement data can be found in Table 3.

Description. Male. Body short, stout, with slightly golden brown colour. Cephalic capsule, the lip region forming a flattened hat on the main capsule region, rectangular shaped, 13–15 μm *22–26 μm, a sutura present seperating capsule and lip region. Cuticle annulated starting just posterior to cephalic capsule. Lateral alae 5–8 μm wide, extending from pharynx posterior end to posterior to cloacal. Six inner labial sensillae and six outer sensilla setiform, 3 μm in length, located on lip region, four cephalic setae, 4–5 μm in length located just posterior to the labial region of cephalic capsule. Eight longitudinal rows of somatic setae, 2–4 μm in length. Amphidial fovea unispiral (30–36% c.b.d.), situated at the main position of cephalic capsule, 6–7 μm from anterior end. Buccal cavity strongly cuticularized with one large dorsal tooth and one small ventrosublateral tooth. Pharynx muscular, with obvious posterior bulb. Nerve ring inconspicuous, at 54–67% of pharynx length. Secretory-excretory system and cardia not found.

Reproductive system monorchic, one anterior testis outstretched located on the right or left of intestine. Spicules slightly curved with small capitulum,1.4–1.6 cloacal diameters in length. Gubernaculum plate-shaped (0.76–1.0 cloacal body diameters) with a cuticularized triangle-shaped lateral piece. Four ventral precloacal copulatory thorns. A pair of ventro-lateral postcloacal thorns, 31–42 μm posterior to cloaca. Tail conical-cylindrical with very short conical portion, 61–76% of tail length. Three caudal glands and spinneret present.

Female. Similar to males in most respects except amphidial fovea smaller (29%–33% c.b.d.). Reproductive system with two reflexed ovaries, located on right side of intestine. Vulva located at posterior portion of the body

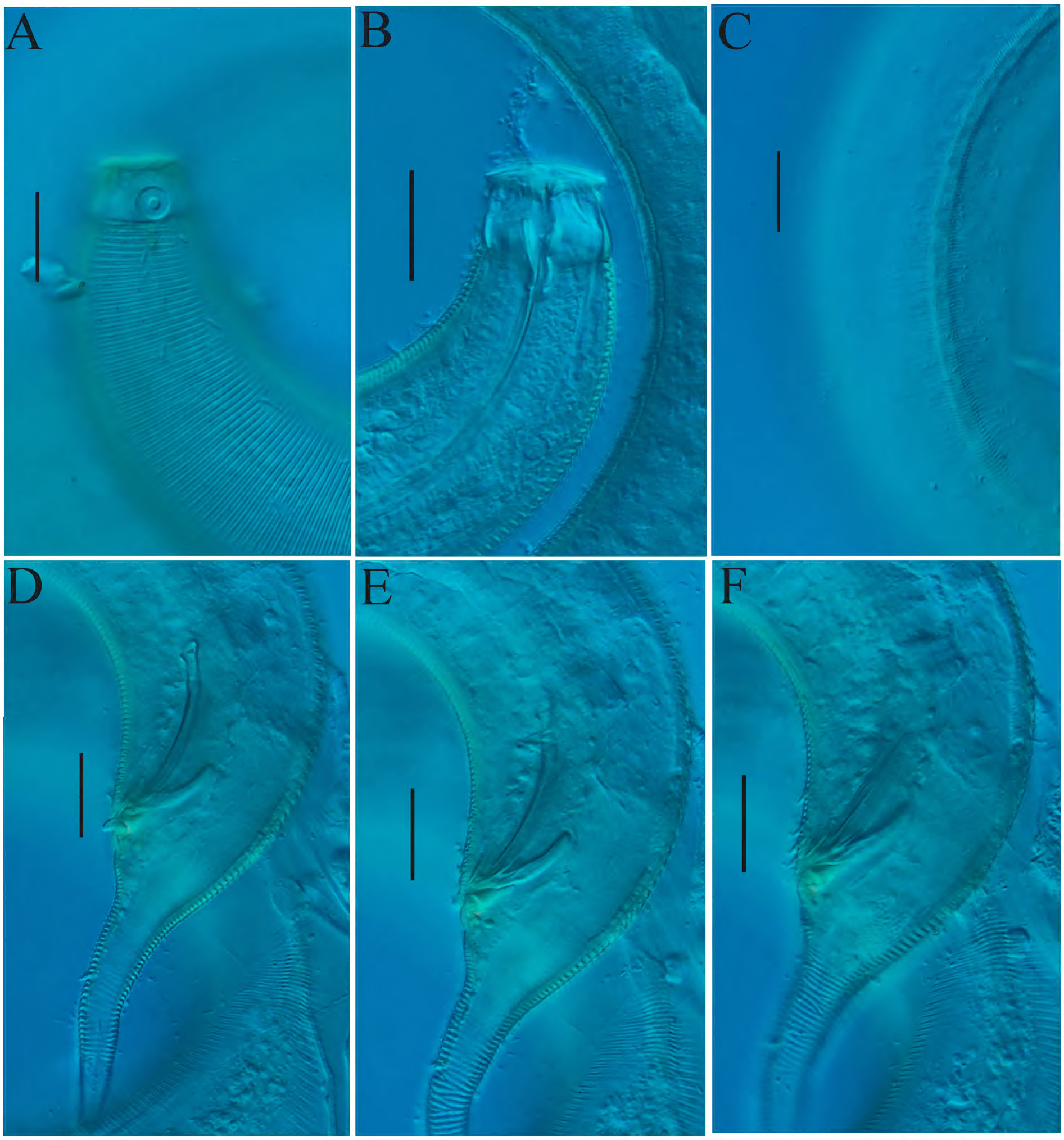

Figure 3. *Pseudochromadora crispata* sp. nov. **A.** Lateral view of the male anterior region, showing amphidial fovea; **B.** Lateral view of the male anterior region, showing cephalic capsule and buccal cavity; **C.** Lateral view of the male alae; **D.** Lateral view of the male posterior region, showing spicules; **E.** Lateral view of the male posterior body, showing gubernaculum; **F.** Lateral view of the male posterior body, showing thorns. Scale bars: 20 μm (**A–F**).

(51–52% of the body length from the anterior end). Vagina surrounded by constrictor muscle. Thorns absent.

Diagnosis. *Pseudochromadora crispata* sp. nov. is characterized by its short body, lateral alae extending from pharynx posterior end to cloacal region, unispiral amphidial fovea, pharynx with obvious posterior bulb, slightly curved spicules, gubernaculum plate shaped with cuticularized lateral piece, four ventral precloacal copulatory thorns and one pair of postcloacal thorns, tail conical-cylindrical with conical portion short.

The new species differs from other species of *Pseudochromadora* in the gubernaculum with triangular lateral piece and copulatory thorn arrangement. *Pseudochromadora crispata* sp. nov. is similar to *Pseudochromadora buccobulbosa* Verschelde & Vincx, 1995, *P. incubans* Gourbault & Vincx, 1990, *P. rossica* Mordukhovich, Fadeeva, Semenchenko & Zograf, 2015 with respect to the shape of spicules, but differs from *P. buccobulbosa* in the buccal cavity (without peri-buccal bulb vs prominent peri-buccal bulb), precloacal copulatory thorns (four in the male, female without thorns vs twenty in the male, five to ten thorns in the female), postcloacal thorns (a pair of thorns in the male vs a ventral group of small thorns), and gubernaculum length (25–30 μm vs 13–18 μm) (Ver-

Table 3. Individual measurements of *Pseudochromadora crispata* sp. nov. (in µm, except ratio).

Characters	Holotype male	Paratypes males (*n* = 4)	Paratypes females (*n* = 3)
Total body length	814	777 ± 93.8(677–863)	796.3 ± 121(690–928)
Maximum body diameter	63	65.3 ± 4(63–70)	60.3 ± 3.5(57–64)
Head diameter	19	19.3 ± 1.5(18–21)	20.7 ± 2.1(19–23)
Length of outer labial setae	4	4.3 ± 0.6(4–5)	3 ± 0(3–3)
Length of cephalic setae	3	3 ± 0(3–3)	2.3 ± 0.6(2–3)
Buccal cavity depth	24	21.3 ± 1.2(20–22)	20 ± 3(17–23)
Amphidial fovea width	8	8 ± 0(8–8)	7 ± 0(7–7)
Amphidial fovea from anterior end	7	6.3 ± 0.6(6–7)	22.3 ± 1.5(6–8)
Body diameter at amphidial fovea	24	24 ± 2.6(22–27)	7 ± 1(21–24)
Nerve ring from anterior end	91	87 ± 9.6(76–94)	83.3 ± 4.6(78–86)
Body diameter at nerve ring	47	48.3 ± 1.5(47–50)	45.3 ± 3.8(41–48)
Pharynx length	146	140 ± 1.7(138–141)	140.7 ± 15.5(128–158)
Body diameter at pharynx base	56	51.3 ± 2.1(49–53)	-
Pharynx bulb length	40	37.7 ± 1.2(37–39)	-
Anal body diameter	34	31.3 ± 1.5(30–33)	26.3 ± 2.3(25–29)
Spicules length along arc	48	47 ± 3.6(43–50)	-
Gubernaculum length	29	27.7 ± 2.5(25–30)	-
Vulva from anterior end	-	-	412 ± 61.7(362–481)
Body diameter at vulva	-	-	60.3 ± 3.5(57–64)
V%	-	-	0.5 ± 0(0.5097–0.5246)
Tail length	79	76 ± 2(74–78)	78 ± 6.1(71–82)
a	12.9	12 ± 2.1(9.7–13.7)	13.2 ± 1.2(12.1–14.5)
b	5.6	5.5 ± 0.6(4.9–6.1)	5.6 ± 0.2(5.4–5.9)
c	10.3	10.2 ± 1.1(9.1–11.4)	10.2 ± 1(9.5–11.3)
c'	2.3	2.4 ± 0.1(2.4–2.5)	3 ± 0.2(2.8–3.2)

schelde and Vincx 1995); differs from *P. incubans* in outer labial setae length (4–5 µm vs 1.5 µm, papilliform), precloacal thorns (four vs three small thorns), gubernaculum length (25–30 µm vs 18–20 µm), tail length (2.3–3.2 c.b.d. vs 3.2–3.8 c.b.d.) (Gourbault and Vincx 1990); differs from *P. rossica* in amphidial width (0.29–0.36 c.b.d. vs 0.19–0.27 c.b.d.), copulatory thorns (4 vs 8–10), and gubernaculum length (25–30 µm vs 15–17 µm) (Mordukhovich et al. 2015).

Systematic of *Microlaimus parakoreanus* sp. nov.

Family Microlaimidae Micoletzky, 1922

Genus *Microlaimus* de Man, 1880

Microlaimus parakoreanus sp. nov.

https://zoobank.org/AD23B2B8-FCB8-4131-A7F1-1CC723DC448C

Figs 4, 5, Table 4

Type material. Four males and three females were measured and studied. Holotype: m#1 on slide 24CJG-2-1-13; paratypes: m#2 on 24CJG-2-1-81, m#3 on 24CJG-2-1-80, m#4 on 24CJG-2-1-13, f#1 on 24CJG-2-1-44, f#2 on 24CJG-2-1-48, f#3 on 24CJG-2-1-76.

Type locality and habitat. All specimens were collected from the Yancheng coast, Jiangsu Province, China. 34°15'N, 120°16'E (CJG), 0–2 cm sediment depth, sandy sediment.

Etymology. The species name refers to the morphological character similar to *Microlaimus korari*.

Measurement. All measurement data can be found in Table 4.

Description. Male. Body spindle shaped. Cuticle striation from cephalic setae to tail tip. Head smooth. Six inner labial sensilla and six outer labial sensilla papilliform. Four cephalic sensilla papilliform. Somatic setae absent. Amphidial fovea cryptocircular, 42–55% c.b.d., from anterior body end. Buccal cavity large, funnel-shaped, heavily cuticularised, with a large dorsal tooth and two small ventrosublateral teeth, small longitudinal cuticularized folds present in cheilostoma. Pharynx posterior portion widened into bulb. Nerve ring at 56–65% of pharynx length. Secretory-excretory system present and excretory pore situated just posterior to nerve ring. Cardia not observed.

Reproductive system paired, testes outstretched and opposed. Anterior and posterior testes to the right of intestine. Spicules curved and faintly cuticularized, proximal end swollen and distal end pointed. Gubernaculum heavily cuticularized, longer than spicules with distal end curving laterally and proximal end swollen.

Precloacal supplements not observed. Tail conical with distal end slightly cylindrical. Three caudal glands and spinneret present.

Females. Similar to males in most respects except amphidial fovea smaller (33%–42% c.b.d.). Reproductive system didelphic and amphidelphic with two ovaries outstretched. Vulva located slightly posterior to mid-body. Vagina short and sclerotized.

Diagnosis. *Microlaimus parakoreanus* sp. nov. is characterized by a striated cuticle, four papilliform ce-

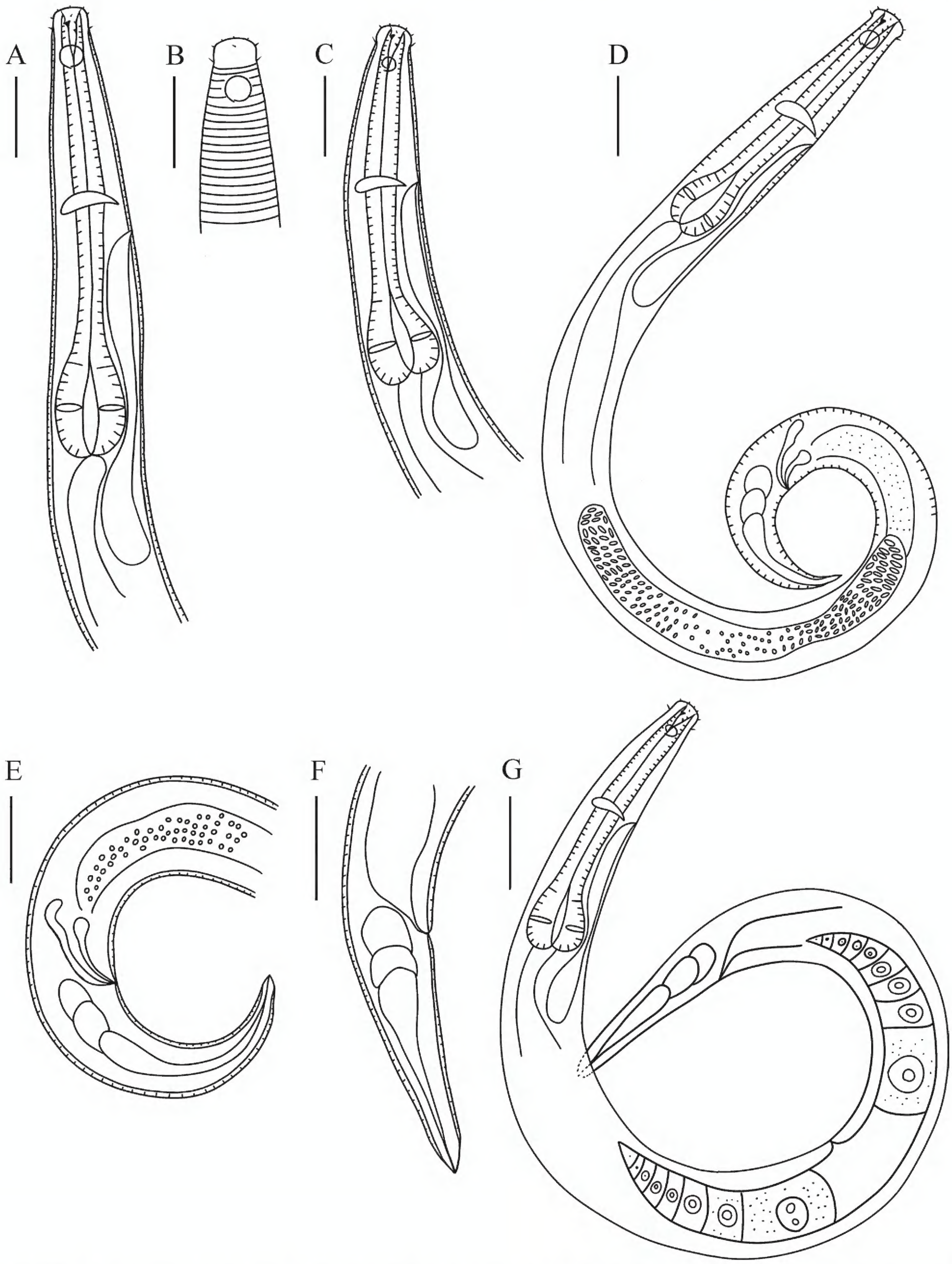

Figure 4. *Microlaimus parakoreanus* sp. nov. **A.** Lateral view of the male anterior region, showing the pharynx region; **B.** Lateral view of the male anterior region, showing amphidial fovea and cuticle; **C.** Lateral view of the female anterior region; **D.** Lateral view of the male entire body; **E.** Lateral view of the male posterior region, showing spicules and gubernaculum; **F.** Lateral view of the female posterior region; **G.** Lateral view of the female entire body. Scale bars: 20 μm (**A–F**); 30 μm (**G**).

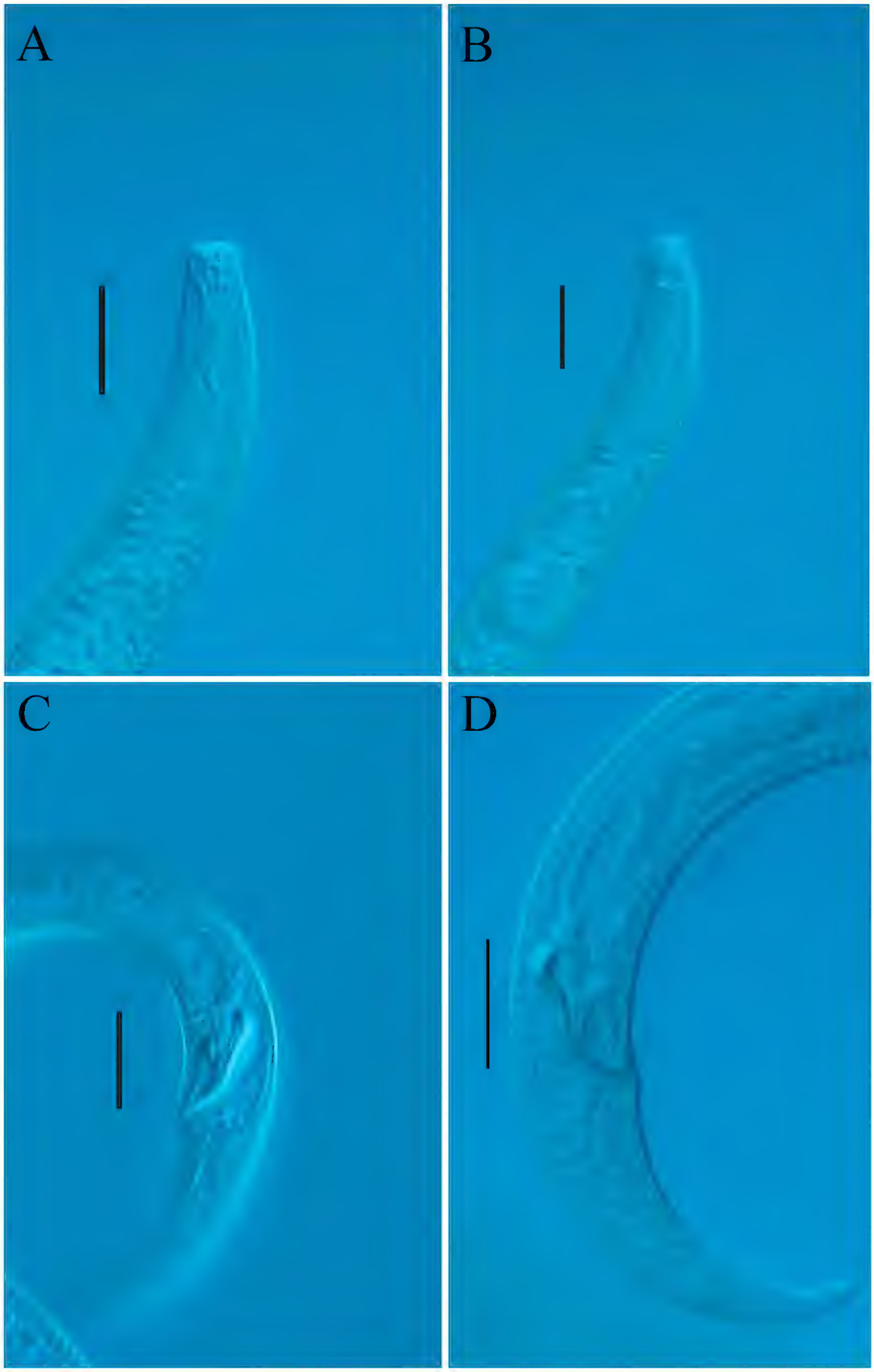

Figure 5. *Microlaimus parakoreanus* sp. nov. **A.** Lateral view of the male anterior region, showing buccal cavity; **B.** Lateral view of the male anterior region, showing amphidial fovea; **C.** Lateral view of the male posterior body, showing spicules and gubernaculum; **D.** Lateral view of the male posterior body, showing tail. Scale bars: 20 µm (**A–D**).

Table 4. Individual measurements of *Microlaimus parakoreanus* sp. nov. (in µm, except ratio).

Characters	Holotype	Paratypes	Paratypes
	male	males (*n* = 4)	females (*n* = 3)
Total body length	473	501.3 ± 46.5(448–533)	481 ± 15.7(463–492)
Maximum body diameter	23	23 ± 1.7(21–24)	27.3 ± 2.9(24–29)
Head diameter	9	9 ± 0(9–9)	9 ± 0(9–9)
Amphidial fovea width	6	5 ± 0(5–5)	4.7 ± 0.6(4–5)
Amphidial fovea from anterior end	9	9 ± 1(8–10)	9.3 ± 1.5(8–11)
Body diameter at amphid fovea	11	11.7 ± 0.6(11–12)	12.3 ± 0.6(12–13)
Buccal cavity depth	12	11 ± 1(10–12)	11.7 ± 0.6(11–12)
Nerve ring from anterior end	56	60.3 ± 7.4(52–66)	21 ± 1.7(20–23)
Body diameter at nerve ring	20	20.7 ± 1.5(19–22)	51.7 ± 3.5(48–55)
Pharynx length	100	98.3 ± 8.1(89–104)	99.3 ± 2.1(97–101)
Pharynx bulb length	23	19.3 ± 1.2(18–20)	23.7±1.5(22–25)
Body diameter at the base of pharynx	22	21.7 ± 1.5(20–23)	24.3 ± 2.5(22–27)
Anal body diameter	19	18.7 ± 1.5(17–20)	17.7 ± 1.5(16–19)
Spicules length along arc	16	18.7 ± 0.6(18–19)	–
Gubernaculum length	26	27.7 ± 1.5(26–29)	–
Vulva from anterior end	–	–	273.7 ± 14.6(258–287)
Body diameter at vulva	–	–	27.7 ± 2.3(25–29)
V%	–	–	0.6 ± 0(0.5572–0.5833)
Tail length	54	60 ± 2.6(57–62)	60.7 ± 2.5(58–63)
a	20.6	21.8 ± 0.4(21.3–22.2)	17.7 ± 1.4(16.8–19.3)
b	20.6	25.9 ± 0.9(24.9–26.7)	20.4 ± 1.6(19.3–22.2)
c	8.8	8.3 ± 0.4(7.9–8.6)	7.9 ± 0.4(7.6–8.4)
c′	2.8	3.2 ± 0.2(3.1–3.4)	3.5 ± 0.3(3.2–3.8)

phalic setae, a buccal cavity with one large dorsal tooth and two small ventrosublateral teeth, amphidial fovea cryptocircular at level of posterior buccal cavity, absence of somatic setae, slightly curved spicules with swollen proximal end, heavily cuticularized gubernaculum, absence of precloacal supplements, conical tail with distal end slightly cylindrical.

The genus *Microlaimus* was recently reviewed by Esteves et al. (2025), and 85 valid species were ascertained. The genus was seperated into seven groups based on spicule length, gubernaculum present or absent, cuticle ornamentation, distance from the anterior edge of amphidial fovea to the anterior end divided by the head diameter (Amph ant/hd). The new species belongs to group 4B with Amph ant/hd ≤1 and amphids diameter < 50% c.b.d.; however, it can be differentiated from the other species in group 4B by the gubernaculum shape. The new species is similar to *Microlaimus korari* Leduc, 2016, in gubernaculum shape but differs in head diameter (9 µm vs 13–15 µm), excretory pore position (situated at or posterior to nerve ring vs situated slightly anterior to nerve ring), and spicule shape (short with proximal end swollen, 0.8–1.1 cloacal body diameters vs long and slender, 2.6–3.8 cloacal body diameters) (Leduc 2016).

Molecular phylogenetic relationships and analysis. The ML topology trees based on rDNA sequences are mostly identical to the BI trees, and only the BI trees are shown in Figs 6, 7. According to Nemys (2025), the family Desmodoridae comprises 48 genera within six subfamilies: Desmodorinae, Pseudonchinae, Molgolaiminae, Spiriniinae, Stilbonematinae, and Prodesmodorinae. Relationships within Desmodoridae were discussed by Armenteros et al. (2014b), Leduc and Verschelde (2015), and Ahmed and Holovachov (2021). Almost all the results considering relationships at the genus level are paraphyletic, consistent with the morphological characters. The family Microlaimidae includes six genera, and relationships within Microlaimidae were discussed by Jensen (1978), Lorenzen (1981), Leduc et al. (2017), and Meng et al. (2025). Microlaimidae was once assigned to Chromadorida, later to Desmodorida, and then transferred to Microlaimida based on molecular evidence. With more molecular sequences available in GenBank, the taxonomic position of Molgolaiminae – consisting of monogeneric *Molgolaimus* – and Prodesmodorinae – consisting of the single genus *Prodesmodora* – could be assessed and clarified at a much wider taxonomic level, including the orders Microlaimida, Chromadorida, and Desmodorida.

Phylogenetic position within Choromadorida, Desmodorida, and Microlaimida

In Fig. 6, 92 sequences of Chromadorida, Desmodorida, and Microlaimida are included, and the three orders – Chromadorida, Microlaimida, and Desmodorida – are shown as paraphyletic clades. In the topology of the rDNA-based phylogenetic tree, *Ixonema* is shown as a separate clade from the Microlaimida group, and its taxonomic position has been discussed by Meng et al. (2025). *Onepunema* is shown as a separate clade from the Desmodorida group, and *Nannolaimoides* and *Xyzzors* deviate from the Chromadorida clade. At the family level, Chromadoridae, Selachinematidae, Cyatholaimidae, Mo-

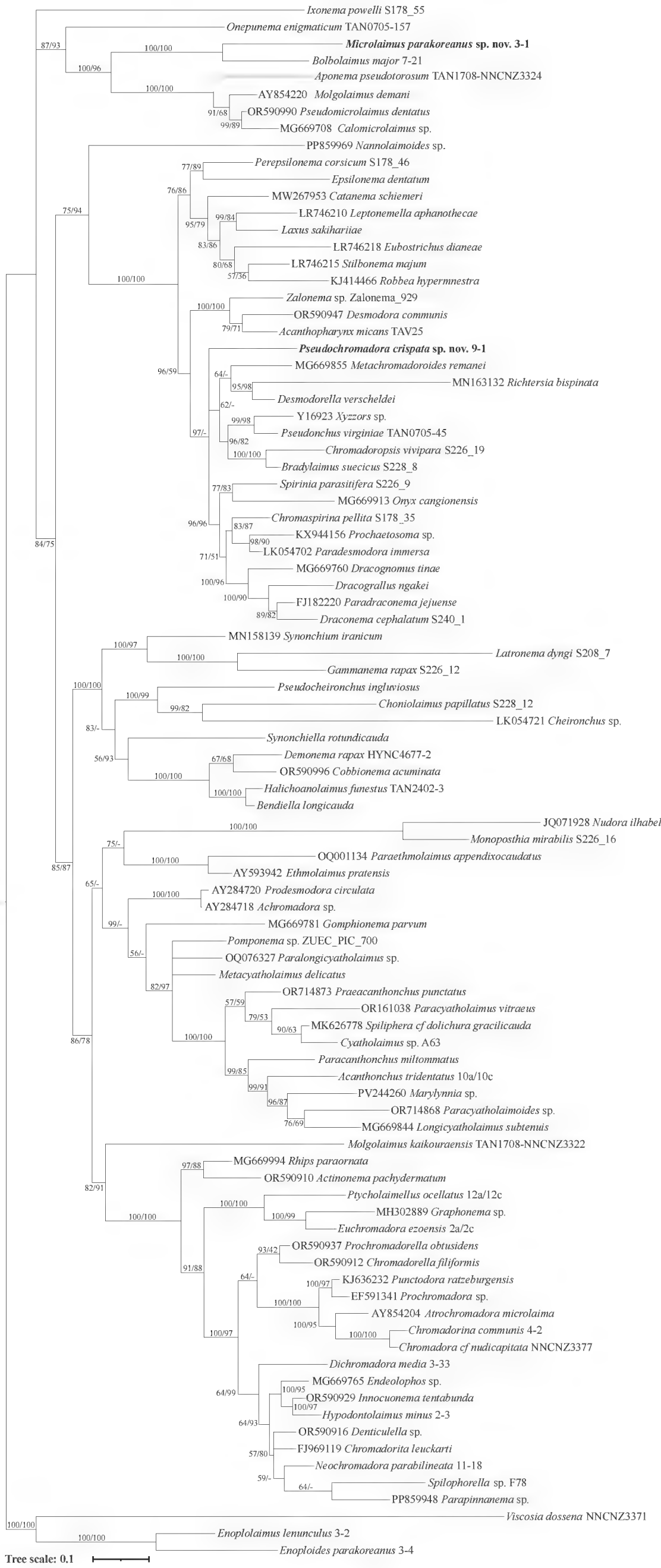

Figure 6. Bayesian inference tree within the Chromadorida, Desmodorida and Microlaimida based on rDNA sequences. Posterior probabilities (left) and bootstrap values (right) are shown for the corresponding clades. Sequences obtained in this study are shown in bold. The scale represents substitutions per site.

noposthiidae, Draconematidae, and Epsilonematidae are shown as monophyletic clades. Sequences of the families Microlaimidae and Desmodoridae are shown as paraphyletic clades.

Morphologically, Draconematidae and Epsilonematidae are considered closely related, with the similar swollen pharyngeal region and mid-posterior body region bearing specialized setae. However, the phylogenetic tree shows that they are in different clades and cluster with Desmodoridae (76% posterior probability and 86% bootstrap value; 71% posterior probability and 51% bootstrap value). Leduc and Zhao (2016) noted that the similarity of adhesion tubes in Draconematidae and ambulatory setae in Epsilonematidae was caused by convergent evolution.

The family Monoposthiidae, constituted by the genera *Nudora* and *Monoposthia*, was placed within Microlaimida by Lorenzen (1994) based on a twelve-fold pleated vestibulum and a prominent dorsal tooth. In the phylogenetic tree, Monoposthiidae does not cluster with Microlaimidae but shows a close relationship with Chromadorida, in accordance with Ahmed and Holovachov (2021) based on SSU evidence. However, according to Holterman et al. (2008) and Leduc et al. (2017), Monoposthiidae clusters with Microlaimidae based on SSU sequences. Species of Microlaimida possess two outstretched ovaries in female specimens (Leduc et al. 2017), whereas *Nudora* and *Monoposthia* have only one reflexed ovary. Considering the importance of the female reproductive system in higher-level taxonomy (Leduc et al. 2019), we propose that these two genera should be removed from Microlaimida based on morphological and molecular evidence. While lacking molecular sequences, the other two genera of Monoposthiidae, *Monoposthioides* and *Rhinema*, should be left in the Microlaimida temporarily.

The taxonomic positions of the genera *Prodesmodora* and *Molgolaimus* are flexible due to their morphological similarities among Chromadorida, Desmodorida, and Microlaimida. The genera *Prodesmodora* and *Molgolaimus* were primarily placed within Microlaimidae for the morphological similarity of the pattern of cephalic setae, the cuticular pattern, the shape of the buccal cavity tooth, and the shape of the amphidial fovea (Jensen 1978). However, Jensen did not account for differences in the pattern of the female reproductive system (reflexed ovary vs. outstretched ovary in Microlaimidae). Lorenzen (1994) and Tchesunov (2014) transferred these two genera to Desmodoridae (Desmodorida) based on their reflexed ovaries.

Species of *Prodesmodora* mainly inhabit terrestrial and freshwater environments. Its taxonomic position has been flexible due to conflicting morphological and molecular evidence. Tchesunov (2014), Leduc et al. (2017), and Hodda (2022) proposed that it should be classified in Desmodoridae based on the presence of reflexed ovaries, while Andrássy (2005) proposed placing *Prodesmodora* in Chromadorida. In our phylogenetic analysis, *Prodesmodora* forms a well-supported clade with the genus *Achromadora* (100% posterior probability and 100% bootstrap value), a group predominantly confined to terrestrial and freshwater biotypes and mostly parthenogenetic. Leduc and Zhao (2016) noted that the terrestrial and freshwater biotype promoted genetic adaptation to a different environment and recommended removing *Prodesmodora* from Desmodoridae. In our previous work (Meng et al. 2025), the biotype was also shown as an important factor – alongside morphological characters – among the three morphologically similar monhysterid genera *Monhystera*, *Halomonhystera*, and *Geomonhystera*. In the topology based on SSU by Zograf et al. (2021), *Prodesmodora* was also shown as a distinct clade separate from the order Desmodorida with long branches. Topologies from van Megen et al. (2009), Leduc and Zhao (2016), and Ahmed and Holovachov (2021) indicate a close relationship of *Prodesmodora* with Chromadorida but not Desmodorida. Considering that cuticle punctations might not be a definitive character for Chromadorida (Leduc et al. 2017), we suggest that the taxonomic position of the genus *Prodesmodora* should be classified within Chromadorida based on molecular evidence.

The genus *Molgolaimus* was originally placed within Microlaimidae (Gerlach and Riemann 1973/1974) based on morphological similarities to the genus *Microlaimus* in the anterior region and the shape of the amphidial fovea, the arrangement of cephalic sensilla, and the structure of the buccal cavity. Later, *Molgolaimus* was transferred to Molgolaimidae (Chromadorida) by Jensen (1978), then to Molgolaiminae (Desmodoridae, Desmodorida) by Lorenzen (1981), and to Molgolaimidae (Microlaimida) based on the molecular evidence of *Molgolaimus demani* by Leduc et al. (2017). However, as noted by the same authors (Leduc et al. 2019), due to overlooking the fact that *M. demani* was accepted as *Microlaimus tenuispiculum*, *Molgolaimus* was transferred to Chromadorida by Leduc et al. (2019) based on the newly added sequence of *Molgolaimus kaikouraensis*.

Currently, two different views regarding the taxonomic position of *Molgolaimus* have been presented, forming a taxonomic dilemma within Chromadorea. Manoel et al. (2025) suggested that *Molgolaimus* should be retained in Desmodorida as proposed by Lorenzen (1994), based on morphological characters and molecular evidence by Sun and Huang (2024). Conversely, Leduc et al. (2019) considered that *Molgolaimus* should be classified in Chromadorida based on molecular phylogenetic analysis. The female reproductive system with two reflexed ovaries makes *Molgolaimus* similar to Chromadorida and Desmodorida but distinct from Microlaimida, which has outstretched ovaries. Additionally, the striated rather than punctated cuticle in *Molgolaimus* shows greater similarity with Desmodorida. However, Leduc et al. (2017) noted that the cuticle pattern might not serve as a differential character at the family or order level. Ultimately, molecular sequence-based phylogenetic analyses, reflexed ovaries in females, and the reduced importance of cuticle pattern in higher taxonomic hierarchy place the

genus *Molgolaimus* within Chromadorida as advocated by Leduc et al. (2019).

The genus *Onepunema* was classified in Desmodoridae based on the characters of both Desmodorinae (thick cuticle, presence of head capsule) and Spiriniinae (small buccal cavity with inconspicuous teeth) (Leduc and Verschelde 2013). The character of two testes in males also distinguished *Onepunema* from other desmodorid genera, which violates the autapomorphy of the superfamily Desmodoroidea, characterized by a single testis. Armenteros et al. (2014a) considered *Onepunema* as taxa incertae sedis. In Fig. 6, *Onepunema* is closely related to Microlaimidae (87% posterior probability and 93% bootstrap value), and in the phylogenetic tree by Zograf et al. (2021), *Onepunema* also separates first from the main clade of Desmodorida. However, the presence of reflexed ovaries and the striated head capsule are totally different from Microlaimida and closely related to Desmodoridae. We suggest that *Onepunema* should be classified temporarily within Desmodoridae based on morphological characters as suggested by Leduc and Verschelde (2015), despite its anomalous phylogenetic position.

The genus *Richtersia* was once placed within Selachinematidae (Chromadorida) by Lorenzen (1994), based on similarities with *Latronema*, which was widely accepted. Tchesunov (2014) noted their difference: the cuticularized ridges of *Latronema* have no spines and are not similar to those of *Richtersia*. This is also supported by LSU-based molecular evidence from Leduc and Zhao (2015). Gharahkhani et al. (2020) transferred Richtersiidae to Desmodorida based on SSU sequences. This is verified in Fig. 6, in which *Richtersia* clustered with the genus *Desmodorella* (95% posterior probability and 98% bootstrap value) with a long branch length.

The placement of *Xyzzors* is also a paradox, as it clusters with the genus *Pseudonchus* (Desmodoridae) (99% posterior probability and 98% bootstrap value) rather than with Cyatholaimidae. This was also noted by Meldal et al. (2007), who suggested its transfer to Desmodoridae. They also discussed SSU limitations in the phylogenetic analysis of Desmodoridae, as it is too conserved to accurately reconstruct relationships.

Phylogenetic analysis within Desmodoridae and Microlaimidae

In Fig. 7, 69 sequences from 28 genera of the families Desmodoridae and Microlaimidae are used to assess the phylogenetic relationships at and within the genus level. In the phylogenetic tree, *Onepunema* clusters with Microlaimidae with a well-supported clade (100% posterior probability and 96% bootstrap value). The genus *Ixonema* forms a separate microlaimid clade clustering with Desmodoridae (95% posterior probability and 86% bootstrap value), as discussed by Meng et al. (2025), based on the unique amphidial fovea shape and a separated spinneret outlet.

The family Desmodoridae is shown as a paraphyletic clade and was reviewed by Leduc and Zhao (2016) and Armenteros et al. (2014a). Desmodoridae was formerly divided into six subfamilies: Desmodorinae, Spiriniinae, Stilbonematinae, Pseudonchinae, Molgolaiminae, and Prodesmodorinae. According to the molecular-based phylogenetic analysis, the latter two subfamilies were transferred to Chromadorida. The remaining four subfamilies in Desmodoridae were shown to be paraphyletic and lack a synapomorphy. The morphological character of Desmodoridae is still defined as members of the Desmodoroidea that lack features of Epsilonematidae and Draconematidae, such as adhesion tubes or ambulatory setae (Lorenzen 1994).

At the subfamily level, three subfamilies – Pseudonchinae (with the only genus *Pseudonchus*), Desmodorinae, and Spiriniinae – cluster together and form a paraphyletic clade. Only species of Stilbonematinae are shown as a weakly supported monophyletic group (53% posterior probability), which is also noted by Armenteros et al. (2014b). Stilbonematinae possesses two synapomorphies: complex glandular sensory organs and symbiosis with chemoautotrophic sulfur-oxidizing bacteria.

Regarding Desmodorinae and Spiriniinae, only three species of the genus *Acanthopharynx* form a monophyletic clade (100% posterior probability and 95% bootstrap value). *Zalonema*, *Paradesmodora*, *Onyx*, *Bradylaimus*, and *Pseudonchus* each consist of only one described species. The genera *Desmodora*, *Pseudochromadora*, *Desmodorella*, *Metachromadora*, *Spirinia*, and *Chromaspirinia* are recovered as paraphyletic groups. This paraphyly was also noted by Armenteros et al. (2014b) and attributed to species misidentification and cryptic species. With an increasing number of species deposited in GenBank, species identification becomes progressively more accurate. Cryptic species provide a more reasonable explanation for paraphyly at the genus level, especially within Desmodorida (Armenteros et al. 2014b).

Three species of *Pseudochromadora* – *P. plurichela*, *P. thinaica*, and *P. crispata* sp. nov. – are included in the tree topology and form a paraphyletic group. *Pseudochromadora plurichela* differs from the other two species by the lateral alae starting position and the absence of a caudal thorn. *Pseudochromadora thinaica* and *P. crispata* sp. nov. possess precloacal and caudal thorns in the male specimen but differ in the shape of the spicules and gubernaculum. Therefore, *P. crispata* sp. nov. should be considered a new species.

Relationships within Microlaimidae have been discussed by Meng et al. (2025) based on the combined sequences of LSU and SSU. The genus *Microlaimus* is also shown as a well-supported paraphyletic group (100% posterior probability and 94% bootstrap value). *Bolbolaimus*, *Calomicrolaimus*, *Pseudomicrolaimus*, and *Aponema* show a close relationship with *Microlaimus* (100% posterior probability and 94% bootstrap value).

Microlaimus parakoreanus sp. nov. forms a well-supported clade with *M. korari* (100% posterior probability

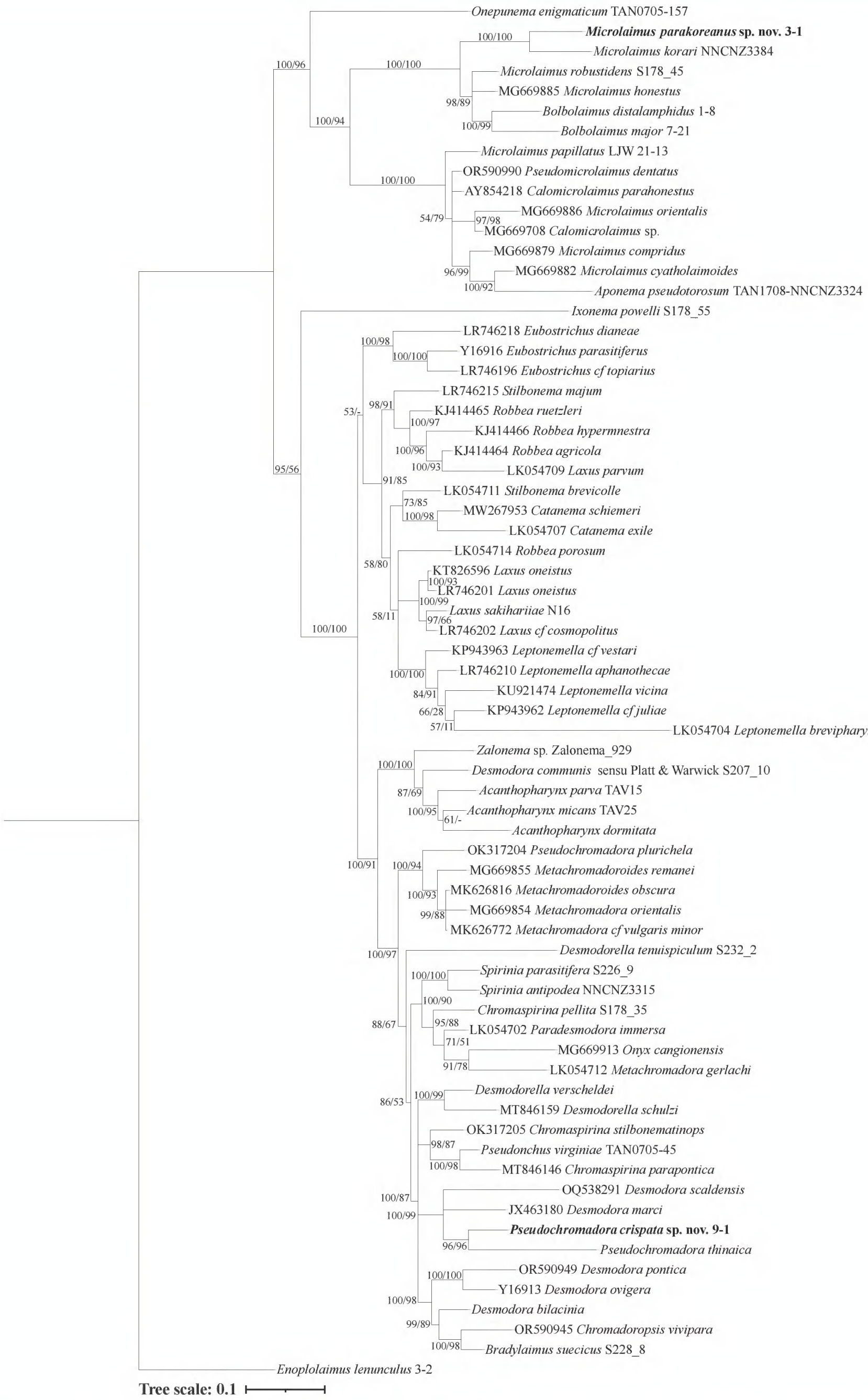

Figure 7. Bayesian inference tree within the family Desmodoridae and Microlaimidae based on rDNA sequences. Posterior probabilities (left) and bootstrap values (right) are shown for the corresponding clades. Sequences obtained in this study are shown in bold. The scale represents substitutions per site.

and 100% bootstrap value). These two species possess similar gubernaculum shape but the spicule length differentiates them easily.

Conclusion

Pseudochromadora crispata sp. nov. is characterized by a short and yellow to brownish body, a unispiral amphidial fovea, lateral alae extending from the posterior end of the pharynx to the cloacal region, a pharynx with an obvious posterior bulb, slightly curved spicules, a plate-shaped gubernaculum with a cuticularized lateral piece, four ventral precloacal copulatory thorns and one pair of postcloacal thorns, and a conical-cylindrical tail with a short conical portion. Phylogenetic relationships based on molecular sequences confirm *P. crispata* sp. nov. as a new species within Desmodoridae. Only Stilbonematinae is shown as a weakly supported monophyletic group; the other three subfamilies are shown as paraphyletic clades, and cryptic species may account for the paraphyly at the genus level.

Microlaimus parakorari sp. nov. is characterized by a medium-sized body, four short cephalic setae, a buccal cavity with one large dorsal tooth and two small ventrosublateral teeth, a cryptocircular amphidial fovea at the level of the posterior buccal cavity, absence of somatic setae, slightly curved spicules with a swollen proximal end, a heavily cuticularized gubernaculum, absence of precloacal supplements, and a conical tail with a slightly cylindrical distal end. Phylogenetic relationships based on molecular sequences confirm *M. parakorari* sp. nov. as a new species within Microlaimidae. Species of *Microlaimus* occur in different clades, and relationships at the genus level are complex and not shown as sister clades to each other.

Phylogenetic analysis within Chromadorida, Microlaimida, and Desmodorida suggests that the genera *Promodesmodora* and *Molgolaimus* should be transferred to Chromadorida based on molecular analysis, the genera *Nudora* and *Monoposthia* should be removed from Microlaimida based on the reflexed ovary and molecular evidence, and *Onepunema* should be kept in Desmodoridae despite its anomalous phylogenetic position.

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